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Long-nights and Moisture Stress Affect Douglas-fir Seedling Growth, Cold Hardiness, Dormancy and Root Growth Potential

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APPLICATION

Nurseries growing 1-year-old Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) seedlings in containers can use long-night (16 hours for 4 weeks) treatments to induce resting bud formation and prepare seedlings for overwinter cold storage (4–6 months at -2°C). Moisture stress, applied as cyclic or constant drought, did not increase the rate of resting bud formation, nor did it affect cold hardiness development or dormancy release. It did, however, result in seedlings with smaller stem diameters, and therefore fewer acceptable seedlings may be expected where culling is based on seedling size.

ABSTRACT

Long-night treatment (16 hours for 4 weeks) reduced height growth of container-grown Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) seedlings by causing the formation of resting terminal buds. Moisture stress caused slight reduction of diameter growth. For between 2 and 14 weeks after long-night treatments ceased, foliage of long-night treated seedlings was approximately 5°C hardier than that on seedlings from other treatments. Moisture stress treatments had no effect on cold hardiness. Long-night treated seedlings, which were stored overwinter, flushed sooner and had higher levels of root growth potential than moisture stressed or non-stressed seedlings. The results of these experiments suggest that long nights are more effective than moisture stress treatments in preparing container-grown Douglas-fir seedlings for overwinter storage.

Keywords: forest nurseries; stock quality; seedling morphology; cold hardiness; root growth potential; dormancy.

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INTRODUCTION

Growing conifer planting stock in containers is widespread in North America, particularly in Canada. This method of forest nursery production allows substantial control over the seedlings' environment such that seedlings of a size suitable for planting (15–25 cm height) can be grown in one 24-week growing season. Successful production of forest planting stock in containers requires a thorough understanding of cultural factors, including temperature, nutrients, moisture supply, daylengths, spacing, growing media and pathogens (Tinus 1982; van Eerden and Gates 1990).

During most of the nursery regime, cultural factors are manipulated to ensure rapid shoot and root growth. Towards the end of the nursery regime, however, the seedlings must be prepared or hardened to withstand either the 4–6 months of cold storage that often precedes field planting or an overwintering out-of-doors at low temperatures. This hardening phase involves the forming of resting buds, lignification of stem tissue and development of cold hardiness.

In seedlings of many conifers, budset and cold hardiness can be most effectively induced through use of long-night treatments (van den Driessche 1970; Cheung 1973; Heide 1974; Timmis and Worrall 1975; Christersson 1978; Sandvik 1980; D'Aoust 1981; Colombo *et al.* 1982; Smit-Spinks *et al.* 1985; O'Reilly *et al.* 1989). Moisture stress induces earlier budset in some species (Lavender *et al.* 1968; Young and Hanover 1978; Macey and Arnott 1986; Arnott *et al.* 1988; O'Reilly *et al.* 1989) and is considered by many nurserymen to be an important tool in hardening container-grown conifer seedlings.

In Douglas-fir, long-night treatments are well known to result in budset and development of cold hardiness (van den Driessche 1969, 1970; Tanaka 1974; Timmis and Worrall 1975). Moisture stress treatments, clearly effective in inducing budset and reducing lammas growth of 2-year-old bareroot-grown Douglas-fir (Lavender 1984), have also been shown to promote bud dormancy of 1-year-old Douglas-fir (Timmis and Tanaka 1976). However, moisture stress may impede cold hardiness development in Douglas-fir (van den Driessche 1969), particularly when extreme moisture stress is used (Blake *et al.* 1979).

These experiments were undertaken to determine the relative effectiveness of long-night and moisture stress treatments in modifying the physical and physiological quality of 1-year-old container-grown Douglas-fir planting stock.

MATERIALS AND METHODS

Plant Material

Interior Douglas-fir seedlings of B.C. Ministry of Forests seedlots 8001 (E. Mad River 51.7°N, 119.7°W 705 m elevation) and 8276 (Summers Creek 49.6°N 120.5°W 1000 m elevation) were grown from seed sown April 28, 1986, for 18 weeks until September 4. The seedlings were grown in styroblock® 4a containers (Beaver Plastics Ltd., Edmonton, Alberta, Canada) having 3 cm diameter and 13 cm deep cells at a spacing of 1000 cells per square metre. Growing conditions in a glasshouse at Vernon, B.C. (50.3°N 119.2°W) were 20–30°C temperatures during 19-hour days and 20°C at night. Minimum light levels of 200 μmol $m^{-2}s^{-1}$ photosynthetically active radiation (PAR) were provided by high-pressure sodium lights. Nutrients were provided through the peat-vermiculite (3:1) growing media being saturated three times each week with soluble fertilizers (9-45-15 and 20-19-18) at rates providing nitrogen at 50 mg L^{-1}. Under these conditions, the seedlings reached approximately 15 cm in height by September 4, 1986, and were in a state of active indeterminate growth.

The experiment was repeated in 1988. The seedlings were raised in the same manner, except they were 14 weeks old at the start of the treatments, having been sown March 22 and grown until June 28.

Treatments

Four styroblocks from each seedlot were randomly assigned to each of the four treatments. The treatments were:

NN – natural night length; no moisture stress

ND1 – natural night length; cyclic drought

ND 2 – natural night length; constant drought

LN – long nights; no moisture stress.

In 1986 and 1988, the long-night and non-stressed treatments (LN; NN) were grown without moisture stress and received 16-hour and natural night lengths, respectively. The long-night treatments in both years were applied for a 4-week period, after which the seedlings were returned to natural night length conditions: 7.5 hours on July 28, 1988, and 12 hours on October 4, 1986. The moisture stress treatments varied in that the constant drought treatment in 1986 was less severe because of the relatively constant 2-kg block weight loss maintained, rather than the 2- to 4-kg block weight loss that occurred in 1988. The cyclic drought in 1986 was more severe than in 1988 because the blocks were allowed to lose 4 kg of water before being rewatered. A weight loss of only 2 kg was aimed for in 1988. Moisture stress treatments also differed between years in that they were applied for a 90-day period in 1986 (September 4 – December 3) and a 66-day period in 1988 (June 28 – September 2).

The mid-day xylem pressure potential of non-moisture stressed seedlings was found to be -0.9 MPa, whereas seedlings taken from styroblocks where a 4 kg weight loss had occurred, had xylem pressure potentials of -2.0 to -2.5 MPa. Pressure-volume analysis (Kandiko *et al.* 1980) indicated that the osmotic potential at incipient plasmolysis (πp) in non-stressed seedlings was between -2.2 and -2.9 MPa. As some seedlings were wilting at this level of moisture stress, it can be assumed that the 4 kg weight loss treatment would cause most seedlings to approach the turgor loss point.

At the end of the treatment period, all seedlings were well watered before being lifted and placed in overwinter storage at -2°C in early December (both years).

Measurements

Samples were collected from each of the four styroblocks within each treatment/seedlot combination. For describing morphology (in 1986 only), 25 seedlings were taken in mid-December and individually measured to determine shoot length, stem diameter at the root collar, shoot dry weight, and root dry weight. For assessing root growth potential (RGP), 10 seedlings were taken in mid-December (in 1986 only), packaged in polyethylene bags, and stored at -2°C inside cardboard cartons lined with polyethylene-coated kraft paper liner bags until early July (approximately 7 months). The RGP test conditions were 30°C day and 25°C night temperatures, with light of 400 $\mu mol\ m^{-2}s^{-1}$ PAR provided for 16 hours during the day period. A peat-vermiculite (3:1) growing medium was used and the seedlings were watered but not fertilized two to three times during the 7-day growing period. To assess root growth, the growing medium was carefully washed away and the number of newly elongated white roots (10 mm and longer) on each seedling's root system were counted.

To measure cold hardiness, on each of several sample dates, 10 seedlings from each styroblock were taken providing four 10-seedling samples for each treatment/seedlot combination. These samples were assigned to be frozen at 6°C hr^{-1} to one of four minimum temperatures (for 1 hour) expected to bracket a temperature that would result in 50% foliage mortality. During the freezing tests, roots were protected from freezing by being potted in moist vermiculite. After freezing and thawing, the seedlings were grown for 7 days in growth chambers providing 25°C day and 20°C night temperatures with 16 hours of light at 200 $\mu mol\ m^{-2}s^{-1}$ PAR. Foliage mortality was assessed for each seedling, and the LT_{50} temperature determined graphically.

To assess terminal budset, 10 seedlings were observed fortnightly between October 1 and December 9 in 1986 and between August 16 and October 25 in 1988. The presence or absence of a resting terminal bud with brown budscales was recorded. In 1988, to determine the treatment effects on terminal

bud dormancy, 20 seedlings from each treatment/seedlot combination were placed into a controlled environment providing 16-hour days with temperatures of 25°C day and 20°C night. Light was provided at 200 μmol $m^{-2}s^{-1}$ PAR during the day period. Budburst was recorded every 2–3 days, and the number of days until 50% of the seedlings' terminal buds had flushed determined. To assess the effect on bud dormancy of overwintering in a cool (above freezing) greenhouse or in -2°C storage, days to 50% budburst were assessed after 0 (December 2), 2 (February 2), and 4 (April 2) months of storage treatment.

Seedling morphology data and root growth potential data were subject to analysis of variance. Treatment effects, where significant, were subject to Duncan's multiple range test using SAS-PC® computer programmes.

RESULTS

Morphology

In 1986, the long-night treatments resulted in the shortest seedlings (Figure 1 and Table 1) which, along with the moisture-stressed seedlings, also had reduced shoot weights compared to the non-stressed seedlings (Figure 2 and Table 1). The moisture stress treatments, particularly the constant drought treatment, reduced seedling stem diameter at the root collar and root dry weights compared to those of seedlings from the non-stress and long-night treatments (Figures 2, 3, and Table 1). Although similar data were not collected in 1988, casual observation suggests that the treatments had similar effects on seedling morphology.

Phenology

On October 17, 1986, and August 16, 1988, nearly all the long-night treated seedlings in both seedlots had formed resting terminal buds (Figure 4). It was not until 4–6 weeks later in both years that the majority of stressed and non-stressed seedlings had formed resting terminal buds. In both 1986 and 1988, Douglas-fir seedlings formed terminal buds after natural night lengths were longer than 10 hours. The moisture stress treatments slightly increased the rate of terminal bud formation compared to that in the non-stressed seedlings. It is unclear why, in 1988, some of the long-night treated seedlings which had formed resting buds resumed growth. However, lammas growth of this sort is not uncommon in Douglas-fir nursery crops where quiescent terminal buds flush in the fall before they can enter maximum rest.

TABLE 1. Analyses of variance for seedling morphology and root growth potential data presented in Figures 1–3 and 6

		Height		Diameter		Shoot weight		Root weight		RGP	
Source	df	MS	F[a]	MS	F	MS	F	MS	F	MS	F
Treatment(T)	3	673.82	9.9***	5.639	24.0***	0.629	2.9^{NS}	0.160	6.7***	2545.64	9.4***
Seedlot (S)	1	1750.25	25.7***	3.295	14.0**	3.907	17.8***	0.156	6.5*	2542.51	9.4**
TxS	3	476.48	7.0**	2.305	9.8***	0.099	0.5^{NS}	0.005	0.2^{NS}	561.22	2.1^{NS}
Error 1 (TxSxRep[S])	24	67.98	7.3***	0.235	2.6***	0.220	2.5***	0.024	2.4***	271.48	1.9**
Error 2	768	9.34		0.089		0.087		0.010		140.36	

[a] Significance of F value; NS = not significant; * = p≤0.05; ** = p≤0.01; *** = p≤0.001.

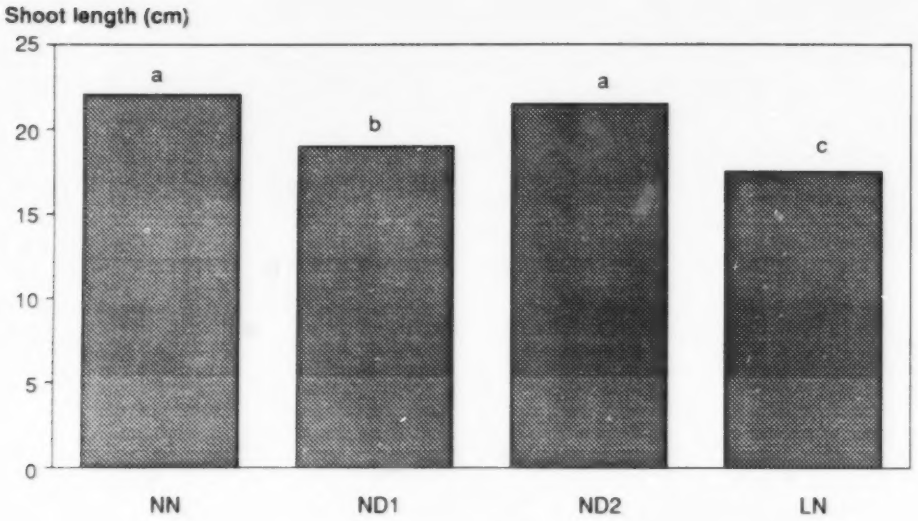

FIGURE 1. Long-night and moisture stress effects on height growth of container-grown Douglas-fir. Treatments are: NN = natural night length and no moisture stress; ND1 = natural night length and cyclic drought; ND2 = natural night length and constant drought; LN = long nights and no moisture stress. Data are pooled for both seedlots 8001 and 8276, with each bar representing the mean height of 200 seedlings. Means not significantly different ($p \leq 0.05$) according to Duncan's multiple range test are indicated with similar letters.

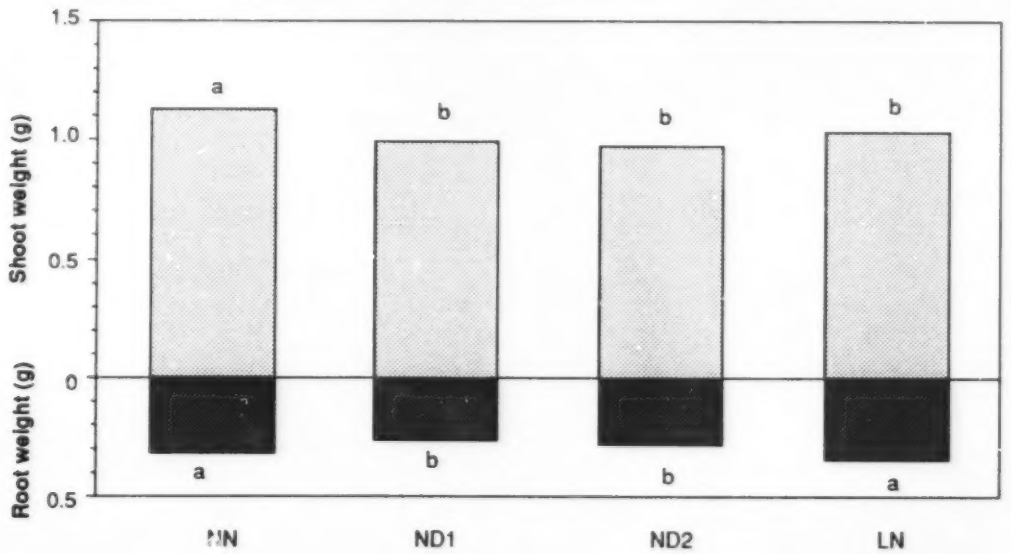

FIGURE 2. Long-night and moisture stress effects on shoot and root dry weight of container-grown Douglas-fir. Treatments are: NN = natural night length and no moisture stress; ND1 = natural night length and cyclic drought; ND2 = natural night length and constant drought; LN = long nights and no moisture stress. Data are pooled for both seedlots 8001 and 8276, with each bar representing the mean dry weight of 200 seedlings. Means not significantly different ($p \leq 0.05$) according to Duncan's multiple range test are indicated with similar letters.

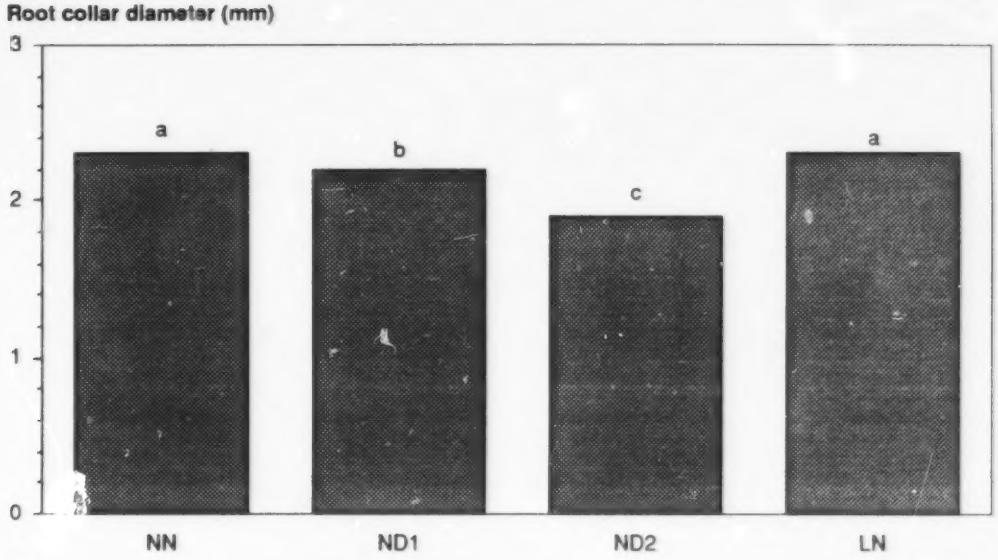

FIGURE 3. Long-night and moisture stress effects on stem diameter of container-grown Douglas-fir. Treatments are: NN = natural night length and no moisture stress; ND1 = natural night length and cyclic drought; ND2 = natural night length and constant drought; LN = long nights and no moisture stress. Data are pooled for both seedlots 8001 and 8276, with each bar representing the mean stem diameter of 200 seedlings. Means not significantly different ($p \leq 0.05$) according to Duncan's multiple range test are indicated with similar letters.

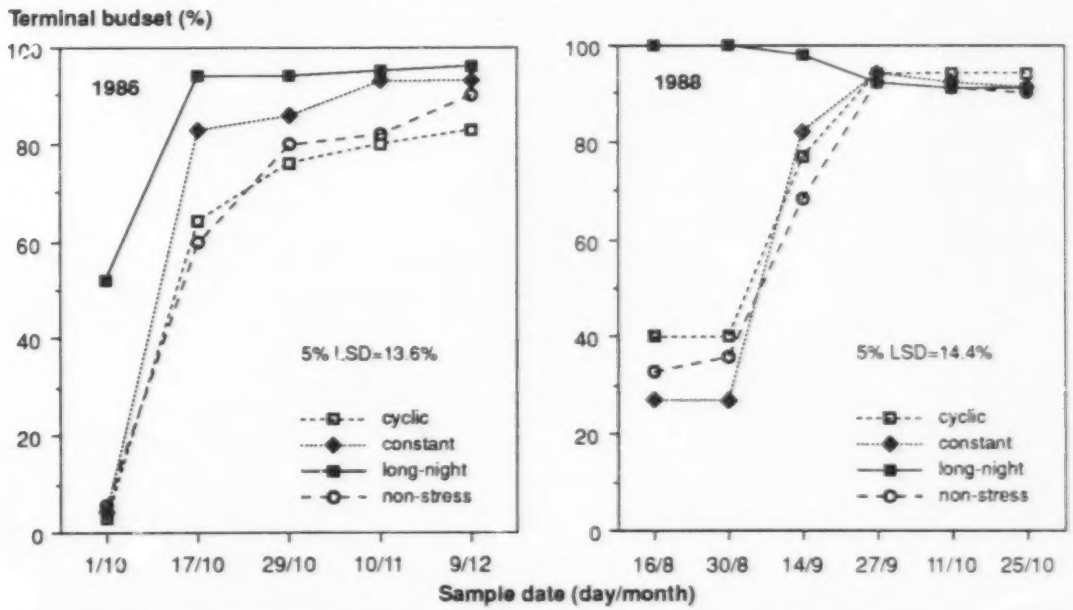

FIGURE 4. Terminal bud formation in container-grown Douglas-fir subjected to cyclic moisture stress, constant moisture stress, long-night, or non-stress hardening treatments. A 5% least significant difference (LSD) is indicated.

Physiology

Long-night treatments caused seedlings to be slightly more cold hardy in terms of foliage LT_{50}. In 1988, all treatments in both seedlots developed substantial foliage hardiness, reaching LT_{50} levels of less than -30°C on the last sample date (November 14) (Figure 5). In the 1986 experiment, LT_{50} values were determined for only the October 23 sample date. The results from this date indicate that the seedlings receiving the long-night treatments had LT_{50} levels of -11.5°C, while the LT_{50} levels of the stressed and non-stressed seedlings were approximately -6°C. On the last sample date in 1986 (December 10), at the coldest freezing temperature tested (-24°C), seedlings from all treatments had less than 25% foliage mortality on average.

Root growth potential of overwinter-stored (1986) seedlings that had received long-night treatments was significantly greater than for moisture-stressed and non-stressed seedlings (Figure 6 and Table 1).

Bud dormancy (days to 50% budburst) of seedlings receiving long-night treatments was less intense (i.e., the seedlings flushed faster) than in drought-stressed or control seedlings. Seedlings that were overwintered in the cool greenhouse and -2°C cold storage flushed more rapidly after 2 — and particularly 4 — months of storage. Greenhouse-stored seedlings flushed faster than the frozen-stored seedlings (Table 2).

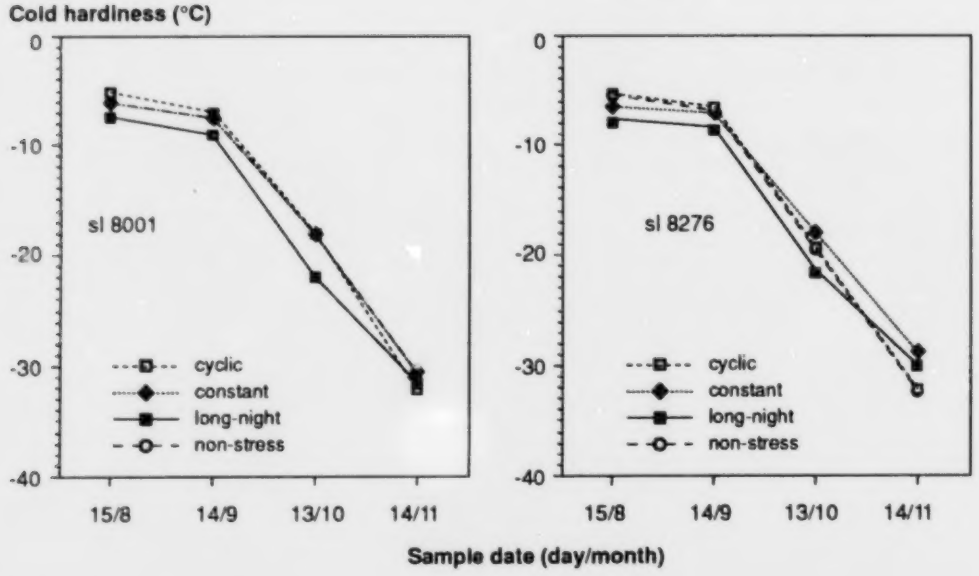

FIGURE 5. Foliage cold hardiness (LT_{50}) of 1988 container-grown Douglas-fir subjected to cyclic moisture stress, constant moisture stress, long-night, or non-stress hardening treatments. Data were determined graphically from results of four freezing tests bracketing each LT_{50} temperature.

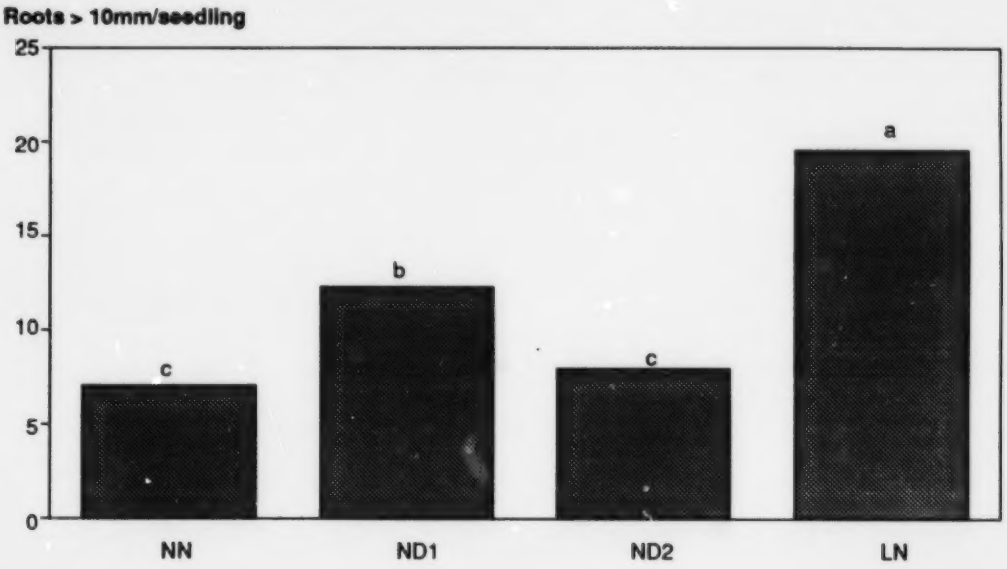

FIGURE 6. Root growth potential of container-grown Douglas-fir seedlings stored for 7 months at -2°C after being subjected to moisture stress and long-night hardening treatments. Treatments are: NN = natural night length and no moisture stress; ND1 = natural night length and cyclic drought; ND2 = natural night length and constant drought; LN = long nights and no moisture stress. Data from seedlots 8001 and 8276 have been pooled so that each bar represents the mean root growth potential of 40 seedlings. Means not significantly different ($p \leq 0.05$) according to Duncan's multiple range test are indicated by similar letters.

TABLE 2. Days to 50% budburst in Douglas-fir seedlings treated with long nights or moisture stress before overwintering in frozen storage (-2°C) or unheated greenhouse conditions

	Storage duration (months)									
	0		2				4			
Storage type			Frozen		Greenhouse		Frozen		Greenhouse	
Seedlot	8001	8276	8001	8276	8001	8276	8001	8276	8001	8276
Non-stress	19	21	16	42	15	14	16	16	5	5
Cyclic drought	38	23	15	16	20	17	16	11	6	6
Constant drought	19	18	14	12	13	13	10	11	5	4
Long-night	16	21	12	16	11	13	6	8	2	4

DISCUSSION

Long-night and moisture stress treatments both affected growth of container-grown Douglas-fir seedlings. Long-night treatments affected shoot height growth by causing resting buds to form. Moisture stress, on the other hand, had little effect on the rate of terminal bud formation, but did reduce seedling stem diameter growth, presumably through reduced cambial growth. Long-night enhancement of resting

bud formation as observed in these experiments is consistent with the findings in previous studies of Douglas-fir (van den Driessche 1970; Timmis and Worrall 1975) and other conifers (Cheung 1973; Heide 1974; Christersson 1978; Sandvik 1980; D'Aoust 1981; Colombo *et al.* 1982; Smit-Spinks *et al.* 1985; Arnott *et al.* 1988). The absence of a moisture stress effect on the rate of resting bud formation, although also noted by Carlson *et al.* (1980), contrasts with the effects reported for Douglas-fir (Timmis and Tanaka 1976) and for spruce species (Young and Hanover 1978; Macey and Arnott 1986).

It should be noted that these previous studies compared bud formation by stressed and non-stressed seedlings under short-night conditions. Under such conditions in a photoperiod-sensitive species such as Douglas-fir, the non-stressed or control seedlings would be expected to continue normal indeterminate growth and not form resting buds. In the experiments reported here, it is likely that the stressed and non-stressed seedlings formed resting buds in response to the naturally lengthening (approximately 10-hour) nights, and the application of moisture stress treatments did not increase the rate of bud formation. Similar lack of response to moisture stress applied under naturally declining photoperiods has been reported in western larch (Vance and Running 1985).

Reduced dry matter accumulation by shoots and roots under moisture stress (Figure 2) may be through lower net photosynthesis caused by reduced stomatal conductance (Blake and Ferrell 1977). The moisture stress effects on cambial growth, seen as smaller stem diameters in the stressed seedlings (Figure 3), are consistent with effects reported by Timmis and Tanaka (1976).

Long-night treatments, although resulting in formation of resting terminal buds, had only a small effect on the development of cold hardiness. Long-night treated seedlings remained slightly hardier through the fall (Figure 5), and the rate of cold hardiness development was similar in seedlings from all treatments. The effect of long-night treatment on cold hardiness development might have been more evident had some of the seedlings been maintained under short-night conditions known to prevent hardening in Douglas-fir (van den Driessche 1970); or had the long-night treatments been applied longer than 4 weeks.

After storage, terminal bud dormancy of seedlings receiving the long-night treatments was less intense than for moisture-stressed or control seedlings (Table 2). This effect on bud dormancy was most evident after 2 or 4 months of storage at -2°C or in a greenhouse at temperatures near 5°C. The long-night treatment made the seedlings more responsive to the dormancy-breaking chilling that the seedlings received either before or during storage. The seedlings subject to constant moisture stress during the hardening period had a slight tendency to be less dormant than the non-stressed or cyclically moisture-stressed seedlings. Consistent with Ritchie's (1984) observations, cold, dark storage did not provide the same satisfaction of the chilling requirements for rapid bud flushing as did overwinter storage in a cool greenhouse.

The results of this experiment further support the importance of allowing sufficient time for the natural dormancy processes to occur, as advocated by Lavender and Stafford (1985). Although sufficient time was permitted to allow cold hardiness to develop equally in all treatments before overwinter cold storage, long-night treated seedlings flushed faster after storage. As seedlings in all treatments received the same amount of pre-lift chilling and yet had different dormancy intensities, it is apparent that the effectiveness of dormancy-breaking chilling is mediated by night length conditions. It is possible that the differences in post-storage root growth potential between long-night treated and the other seedlings are also due to interaction with long-night mediated endogenous processes which reduce the effectiveness of chilling temperatures on roots before and during storage.

It is equally possible, however, that the long-night treatments affected the photosynthetic ability of the seedling such that either long-night treated seedlings' photosynthetic systems were less affected by storage conditions (Mattsson and Troeng 1986) or that, on removal from storage, long-night treated seedlings were able to produce more current photosynthate. Recently it has been shown (van den Driessche 1987; Philipson 1988) that root growth potential in Douglas-fir seedlings depends closely on current photosynthate.

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